Digestive physiology of the plains viscacha (Lagostomus maximus): a large herbivorous hystricomorph rodent

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Digestive Physiology of the Plains Viscacha (*Lagostomus maximus*), a Large Herbivorous Hystricomorph Rodent

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Running head: Viscacha digestive physiology

Abstract

Plains viscachas (*Lagostomus maximus*) are large South American, fossorial rodents susceptible to diabetic cataracts. Various aspects of their digestive physiology were studied in three different experiments with 9 male and 7 female adult animals and 6 different diets (total n of feeding trials = 35). Viscachas achieved mean retention times of 23-31h, which is of a magnitude also recorded in horses; these did not differ for solute or small particle (<2mm) markers. Secondary marker excretion peaks indicated coprophagy, and were rarer on high-protein as compared to grass hay-only diets. Mean resting metabolic rate was, at 229 $kJ/kg^{0.75}/d$, lower than expected for a mammal of this size. Digestible energy requirement for maintenance was 445 $kJ/kg^{0.75}/d$. At 1.6-2.7 L/d, viscachas produced more methane than expected for a hindgut fermenter of their size. On diets that included concentrate feeds, viscachas excreted glucose in their urine, corroborating reports on the susceptibility of this species for diabetes when kept on energy-dense food. Viscachas had a similar apparent digestibility of protein, lipids, and macrominerals as other rodents, rabbits, or domestic horses. This suggests that whether or not a species practices coprophagy does not have a major influence on these measures. Viscachas resemble other hindgut fermenters in their high apparent calcium digestibility. With respect to a digestibility-reducing effect of dietary fiber, viscachas differed from rabbits and guinea pigs but were similar to horses, suggesting that small body size needs not necessarily be linked to lower digestive efficiency on high-fiber diets.

Key words: herbivory, nutrition, colonic separation mechanism, coprophagy, obesity

INTRODUCTION

In the debate on the influence of body size on digestive physiology, niche differentiation and species diversification, the traditional focus has been on large ungulate herbivores with well-documented differences in diet type and diet quality [Clauss et al., 2013]. Efficient herbivory has long been considered a privilege of large-bodied mammals [Demment and Van Soest, 1985; Foley and Cork, 1992], and herbivorous small mammals such as rodents appear less intensively studied [Smith, 1995]. However, many rodent species are true herbivores [Wilman et al., 2014] and have developed a variety of corresponding morphological and physiological adaptations [Gorgas, 1966; Cork et al., 1999; Sakaguchi, 2003] that need to be understood for a full assessment of strategies facilitating herbivory. These adaptive mechanisms comprise selective feeding [Justice and Smith, 1992]; a strategy of compensatory high food intake as diet quality declines [Meyer et al., 2010]; large relative gut capacities similar to those of larger mammals; digesta retention times that are similar to, or lower than, those of larger mammals [Müller et al., 2013]; different strategies with respect to the movement of fluids and particles in the colonic separation mechanism that facilitates the strategy of coprophagy [Hume and Sakaguchi, 1991; Franz et al., 2011a]; microbial fiber fermentation [Stevens and Hume, 1998]; a strategy to absorb more calcium than required from the intestinal tract and excrete the surplus via urine [Hagen et al., 2015]; and a relative methane production similar to other nonruminant mammals [Franz et al., 2011b].

Plains viscachas (*Lagostomus maximus*) are hystricomorph South American rodents that occur in a variety of arid, semiarid or humid habitats; they are colonial and live in a communal burrow system [Jackson et al., 1996]. Plains viscachas have a colonic furrow typical for hystricomorph rodents [Gorgas, 1966], practice coprophagy [Jackson et al., 1996; Clauss et al., 2007] and are able to concentrate urine similar to desert rodents [Kohl, 1980]. They are herbivorous [Campos et al., 2001], with an apparent preference for grasses [Giulietti and Jackson, 1986; Branch et al., 1994; Puig et al., 1998; Bontti et al., 1999; Pereira et al.,

2003], and have been reported to have a low metabolic rate [Kohl, 1980]. Nevertheless, their diet in captivity has traditionally contained varied amounts of energy dense feeds, which may trigger diet-induced diabetes mellitus with cataract formation, similar to degus (*Octodon degus*) [Rübel et al., 1989; Gull et al., 2009; Wenker et al., 2009].

In the course of investigating the nutritional requirements of this species, the various experiments reported in the present study were performed. The overall aim was to facilitate a comparison of the plains viscacha with other herbivores, to assess convergence or homology in digestive function. In particular, we aimed to test, in a comparison with domestic horses, whether differences in the digestive efficiency can be demonstrated that are either putatively related to (i) body mass (the influence of dietary fiber on digestive efficiency) or (ii) to digestive strategy (assuming higher apparent digestive efficiency for protein and lipids in a coprophageous vs. a noncoprophagoues herbivore).

MATERIALS AND METHODS

Experiment 1: Anatomy of the Digestive Tract

Experiment (Exp) 1 involved two male and two female adult plains viscachas (Table 1) euthanized at a zoological facility for management reasons. The animals were weighed, their body length was recorded (as the distance from snout to the base of the tail), the digestive tract was dissected, freed from mesenteries, and the length and masses of individual gut sections and their contents were measured.

Experiments 2-4: Diet Effects

In Exp 2-4, carried out between 2003 and 2013, three different feeding approaches were tested. The experiments were approved by the cantonal veterinary office (licenses no. 194/2003, 119/2005, 142/2011). Exp 2 was performed with four male and three female adult plains viscachas, each subjected to two dietary treatments, consisting of an *ad libitum* grass

hay-only diet (Exp 2A) and a diet where grass hay was supplemented with 40 g (as fed) per kg body mass of commercial Guinea pig pellets (Kliba NAFAG, Kaiseraugst, Schweiz) and 40 g (as fed) per kg body mass of carrots (Exp 2B) (diet composition: Table 2). Exp 3 was performed with three different adult male and female viscachas, respectively, each undergoing three dietary treatments, consisting of two grass hay-only diets (Exp 3A and C) and a diet where grass hay was supplemented with a different commercial pelleted food in between (Exp 3B). Exp 4 was performed with three different adult male viscachas fed a diet consisting of lucerne (alfalfa) hay and pellets from lucerne.

Food Intake and Digestibility

These three experiments included adaptation periods to the respective diets of 7 days (Exp 2), 8 weeks (Exp 3) or 14 days (Exp 4). Animals were housed individually in various enclosure types provided with a den-like shelter and water *ad libitum*. Collection periods lasted for at least 5 days. Food intake was quantified by weighing food offered and leftovers, and fecal output was quantified by total fecal collection. Daily samples leftovers and feces were pooled per animal feeding period, and thoroughly mixed to yield representative samples for analysis; similarly, the hays used were sampled daily to yield a sample representative for one feeding period. When sampling feces, those fecal pellets evidently contaminated by urine were discarded. In Exp 2 and Exp 4, adaptation periods and collection periods were performed in the same enclosures (1.2-2.0 m^2, at ambient temperatures of 20-22°C). In Exp 3, animals were transferred to cages (0.35-0.58 m^2) with a mesh floor for the last days of adaptation and the collection periods (at ambient temperatures of 5-15°C) in order to facilitate urine collection. Due to the visual impression that individual fecal pellets were distinctively smaller in Exp 3B than in Exp 3A, ten randomly selected individual fecal pellets were weighed per animal in Exp 3B and C. In Exp 3, water intake was quantified by weighing water offered and left over (accounting for evaporation losses using a control dish), and urine was collected completely

from a funnel system attached underneath the wire mesh cages and the finer mesh where feces were retained. The composition of leftover hay was only analyzed in Exp 3 and Exp 4.

Samples were subjected to standard nutrient analyses [AOAC, 2012] in duplicate for dry matter (DM) and total ash (AOAC no. 942.05), crude protein (CP, AOAC no. 977.02), ether extract (AOAC no. 963.15), crude fiber (CF, AOAC no. 930.10) as well as neutral detergent fiber (NDF, AOAC no. 2002.04), acid detergent fiber (ADF) and acid detergent lignin analysis (AOAC no. 973.18). All fiber values are expressed without residual ash. Gross energy (GE) was determined by bomb calorimetry (IKA-Calorimeter C4000, Ika, Stauffen, Germany). Concentrations of sodium (Na), potassium (K), calcium (Ca), phosphorus (P), magnesium (Mg), copper (Cu) and zinc (Zn) were analyzed in Exp 2 and 3. To 0.5 g of sample, 5 ml of 65% HNO_3 was added for wet ashing (1200 mega High Performance Microwave, MLS, Milestone, Leutkirch, Germany). The minerals Ca, Na and K were analyzed by flame photometry (EFOX 5053, Eppendorf, Hamburg, Germany), P by spectrophotometry (using ammonium molybdic acid and ammonium vanadic acid, 1:1; GENESYS 10 UV, Thermo Spectronic, Dreieich, Germany), and Cu and Zn by atomic absorption spectroscopy (AAnalyst 800, Perkin-Elmer, Waltham, MA, USA). In Exp 2, metabolic fecal nitrogen was determined according to Schwarm et al. [2009]. Apparent digestibilities were calculated as the proportion of a nutrient not excreted of the overall intake [Robbins, 1993]. To facilitate comparison with data from other species, the concentration of a nutrient was plotted against the concentration of the digestible fraction of that nutrient [Clauss et al., 2008; Clauss et al., 2010b].

Mean Retention Time

The mean retention times (MRT) of a solute marker (cobalt-EDTA) and a particle marker (chromium-mordanted fiber particles <2mm), prepared according to Udén et al. [1980], were measured. Markers were fed as a pulse-dose, and sampling of feces was performed at regular

intervals afterwards. Feces were analyzed for markers either using atomic absorption spectroscopy as described by Behrend et al. [2004; Exp 2 and 3] or inductively coupled plasma optical emission spectrometry as described by Frei et al. [2015; Exp 4]. The MRT through the whole digestive tract was calculated according to Thielemans et al. [1978] as

$$MRT = \frac{\Sigma\, t_i\, C_i\, dt_i}{\Sigma\, C_i\, dt_i}$$

with C_i = marker concentration in the fecal samples from the interval represented by time t_i (h after marker administration, using the midpoint of the sampling interval) and dt_i = the interval (h) of the respective sample

$$dt_i = \frac{(t_{i+1}-t_i)+(t_i-t_{i-1})}{2}$$

The marker was assumed to have been excreted completely once the fecal marker concentrations were similar to the background-levels determined in pre-dose fecal samples.

Diabetes Indicators in Urine and Blood

Urine samples were available from spontaneous urinations or urine gained by applying gentle transabdominal pressure on the bladder under isofluorane anesthesia [Wenker et al., 2007] at the end of each collection period in Exp 2, or from total collection in Exp 3. Urinary glucose concentration was estimated with a commercial test strip (Combur-Test, Roche Diagnostics AG, Rotkreuz, Switzerland; graded at 1 = below detection limit, 2 = 2.8, 3 = 5.6, 4 = 16.7 and 5 = 55.5 mmol/L). Blood samples were taken under isofluorane anesthesia at the end of each collection period in Exp 2 and 3 from the *Vena femoralis* and centrifuged to gain serum, which was analyzed for glucose and fructosamine concentrations in a Cobas-Integra 700 Analyzer (Roche-Diagnostics, Rotkreuz, Switzerland). Additionally, urinary glucose was measured in Exp 3B/C using the same equipment.

176 *Respirometry*

177 After completion of the collection period, the three animals of Exp 4 were transferred to
178 respiration chambers (49 x 59 cm floor, 40 cm height) that had served as shelter in their
179 enclosures during the preceding period. Chambers were filled with amounts of lucerne hay,
180 lucerne pellets and water sufficient to allow *ad libitum* consumption. Air inlets on the bottom
181 and air outlets on top of the chambers ensured a constant airflow (10 L/min) generated by an
182 attached pump (Flowkit 100, Sable Systems, Las Vegas, USA). Flexible hoses ducted the out-
183 flowing air to a gas multiplexer, which allowed the measurement of all three individuals and
184 as well as ambient air (to determine base line gas values), at alternating intervals of 90 s each.
185 Concentrations of O_2 and CO_2 were analyzed by a Turbofox (Sable Systems). Methane was
186 measured by a MA-10 Methane Analyzer (Sable Systems). Data were adjusted for barometric
187 pressure, water vapor pressure and air flow rates, which were constantly recorded during
188 respirometry (Turbofox, Sable Systems). Gas analyzers were manually calibrated with
189 calibration gases (pure N_2, and a mixture containing 19.91 % O_2, 0.5032 % CO_2, 0.4945 %
190 CH_4 dissolved in N_2). Data obtained by the respirometry system were analyzed with the
191 software ExpeData (Sable Systems) for O_2 consumed and CH_4 and CO_2 emitted after
192 correcting for gas concentrations in incoming air.

193 The mean metabolic rate (MR) was calculated based on the entire 23-h measurement
194 period, therefore accounting for the activity of the animals inside the box, while the resting
195 MR (RMR) of the animals was calculated by selecting the 20 lowest O_2 measurements per
196 individual within the entire measurement [adapted from Derno et al., 2005]. Data from the
197 first hour the animals spent inside the respiration chambers were neglected. In order to
198 estimate MR, the amount of O_2 consumed (in L/h) was multiplied by 20.08 kJ [McNab, 2008].

199

200 *Statistical Analysis*

For comparative purposes, data collected by Hagen et al. [2015] were used. Data were analyzed, as appropriate, by parametric or nonparametric tests for paired measurements, using Sidak correction for multiple testing when indicated. Analyses were performed in SPSS 21.0 (SPSS Inc., Chicago, IL), with the significance level set to 0.05.

RESULTS

The digestive tract of the plains viscachas investigated was characterized by a simple stomach, a voluminous cecum, a *colon ascendens* with a colonic furrow whose borders were defined by simple muscular ridges, and a long descending colon (view of the digestive tract of one individual in Fig. 1). The wet mass of total gut contents represented 11.0 ±3.5 % of body mass (Table 1).

There was no pronounced feeding selectivity in the animals in Exp 3 (Table 2), because the hay ingested did not differ from the hay offered in terms of contents of CP, CF or NDF. The relative dry matter intake (rDMI) varied, across experiments, from 38 to 51 $g/kg^{0.75}/d$ (Table 3) and was not correlated to either dietary fiber content or organic matter digestibility. There was no difference in rDMI between Exp 2A and Exp 2B. In contrast, rDMI in Exp 3A was higher than that of Exp 3B or Exp 3C (paired t-test with Sidak adjustment, $P=0.001$ and 0.014, respectively), with no difference between the latter two. Total water intake (only measured in Exp 3) was closely correlated to DMI ($R=0.86$, $P<0.001$) (Fig. 2); it averaged at 1.2 ±0.3 g/g DMI, which was lower than reported for guinea pigs, degus, chinchillas and rabbits on diets consisting of dry food (Fig. 2). However, the only significant difference was between guinea pigs and all other species (ANOVA and Sidak post hoc tests, $P<0.001$ for comparisons with guinea pigs, $P>0.05$ for all other comparisons).

Particle and solute MRT ranged at 23-31 h (Table 3) and were highly correlated with each other ($R=0.93$, $P<0.001$). There was no difference in the MRT of particles and solutes, and no relationship between body mass, rDMI or relative water intake on the one hand and

MRT measures on the other hand. Behavior compatible with coprophagy was observed sporadically (Fig. 3). In addition, the marker excretion patterns showed several secondary peaks suggesting that coprophagy took place on the grass hay diets (Exp 2A and 3A) but less so on the pelleted diet (Exp 2B) or the lucerne hay diet (Exp 4) (Fig. 4). When comparing repeated measurements in individuals on two diets, animals had a higher number of secondary marker excretion peaks (median 3, range 2-5) in Exp 2A than in Exp 2B (median 2, range 1-3; Wilcoxon signed rank test, P=0.024).

There was a difference in the relative fecal dry matter excretion between Exp 2A and Exp 2B (paired t-test, P=0.002), and between Exp 3B and Exp 3A/C (paired t-test with Sidak adjustment, P<0.001/0.002) but not between the latter two (Table 4). For the two treatments where the individual fecal pellet mass was measured, there was a difference, with larger fecal pellets on the hay-only diet (Exp 3B: 1.82 ±0.61 g; Exp 3C: 2.82 ±0.61 g; paired t-test, P<0.001).

There was no difference in urine excretion between the diet treatments in Exp 3 (Table 4). No urinary glucose, as estimated semi-quantitatively by the Combur test, was found in Exp 2A (n=4), but it had a median level of 30.5 mmol/L (n=6) in Exp 2B, with sample size being too low for statistical testing. Similarly, no urinary glucose was found in all animals of Exp 3A and Exp 3C, but it had a median level of 27.8 mmol/L (n=6) in Exp 3B, with the difference between treatments being significant at P=0.050 (Friedman's ranked ANOVA). Urinary glucose measured quantitatively in the laboratory had a median (range) of 6.0 (2.9-938.4) mmol/L for Exp 3B and 0.2 (0-0.6) mmol/L for Exp 3C, with a significant difference (Related Sample Wilcoxon Rank test, P=0.028).

Serum glucose and fructosamine levels increased numerically but were not statistically different between Exp 2A and Exp 2B (6.5 ±1.0 vs. 6.7 ±1.3 mmol/L and 255 ±24 vs. 281 ±25 µmol/L, respectively). Concentration of serum glucose was 8.5 ±2.1, 9.0 ±4.0 and 7.3

252 ±1.1 mmol/L, and of serum fructosamine was 333 ±33, 354 ±108 and 300 ±26 µmol/L in Exp
253 3A, B and C, respectively, and there were no significant differences between treatments.
254 There was a significant negative correlation (R=-0.76, P<0.001) between dietary crude
255 fiber and the apparent digestibility of organic matter in the viscachas. The relation was
256 different from the relationship of these measures in rabbits and guinea pigs, with a difference
257 in the slope (Table 5), but similar to that in horses (Fig. 5). In contrast, the relationship of
258 nutrient content and digestible nutrient content in the diet did not differ markedly between
259 species for crude protein, ether extracts and minerals (Fig. 6). Confidence intervals for
260 parameter estimates from the corresponding regression equations showed a large degree of
261 overlap (Table 5). Concentration of fecal nitrogen ranged from 1.1 to 3.0 % of DM (mean 1.9
262 ±0.6) (Table 4) and was positively correlated with the apparent digestibility of organic matter
263 (R=0.71, P<0.001).
264 Although the three viscachas of Exp 4 consumed food in the respiration chambers, the
265 respiration quotient was comparatively low (Table 6). Methane production averaged at 2.01
266 ±0.64 L/d and at 3.4 ±1.3 % of gross energy intake (Table 6). The mean resting metabolic rate
267 was determined at 229 ±31 $kJ/kg^{0.75}/d$. Plotting digestible energy (DE) intake versus daily
268 body mass changes from data obtained in Exp 2 resulted in an estimated maintenance DE
269 requirement of 445 $kJ/kg^{0.75}/d$. When adding the data from Exp 3, the requirement estimate
270 increased to 564 $kJ/kg^{0.75}/d$ (Fig. 7).
271
272 **DISCUSSION**
273 The results of the present study characterize and confirm the plains viscacha as a typical
274 herbivorous rodent with a comparatively high digestive efficiency, a mucus-trap colonic
275 separation mechanism, a digestive strategy that includes a flexible degree of coprophagy, a
276 calcium metabolism like many other herbivorous hindgut fermenters, a low metabolic rate,
277 and a susceptibility to diet-induced diabetes.

Limitations of the Present Study

A common challenge in digestion experiments with rodents is the potential contamination of feces with urine, even when animals are kept in metabolism cages. This may not be noticed at the time the feces are collected because the urine may have already dripped off the fecal pellets. Urinary components nevertheless contaminate the fecal sample and hence lead to lower apparent digestibility values for the respective nutrients [Hagen et al., 2015]. Two seeming outliers that had a particularly low apparent digestibility of protein, potassium, calcium and phosphorus (but notably not for lipids that are not excreted via urine, Fig. 6) might represent such cases. Thus, the habit of many rodents to deposit urine directly on their own feces may render digestibility measurements, especially those of minerals, problematic.

Selective feeding behavior can play an important role in the digestive strategy of rodents [Justice and Smith, 1992]. For example, differences in the degree of feeding selectivity could be demonstrated between rabbits and guinea pigs [Franz et al., 2011a]. However, the experimental setup and the diet used will influence possible measurements. The body size of the plains viscachas makes a selective feeding on pelleted diets unlikely, in contrast to what has been reported for smaller rodents [Justice and Smith, 1992; Cameron and Speakman, 2010]. However, the feeding of dried forages might represent challenges. For example, the lower crude protein and higher fiber levels of the lucerne hay ingested as compared to the hay offered in Exp 4 (Table 2) are best explained by crumbling losses of leafy components. On the one hand, the lack of evident feeding selectivity in Exp 3 and Exp 4 suggests that the results of Exp 2 are not unduly compromised by the lack of nutrient analyses of leftovers, and is consistent with observations that plains viscachas apparently do not selectively target the most easily digestible plants in their natural habitats [Branch et al., 1994]. On the other hand, it might be interesting to investigate whether different ways of *ad libitum* feeding can influence results on feeding selectivity. *Ad libitum* feeding is achieved by ensuring that there

304 are always leftovers the next time a diet item is replaced. Yet, for practical reasons, feeding is
305 usually organized in such a way that these leftovers are of a limited amount, and hence
306 typically do not exceed the amount consumed by the animals. Offering diets in much greater
307 abundance, i.e. where leftovers exceed the amount consumed in different degrees of
308 magnitude, might result in different selection opportunities and therefore have an influence on
309 measures of feeding selectivity that has not been evaluated to date.
310 Another limitation is the collation of data from different individual experiments. In the
311 present Exp 3, conditions were different compared to the other experiments, both in terms of
312 ambient temperature and the holding facilities. According to the results of Kohl [1980], the
313 animals of Exp 3 were challenged in their temperature regulation, which might have
314 contributed to generally higher body mass losses at similar DE intakes as compared to Exp 2
315 (Fig. 7). Additionally, housing conditions of Exp 3, in which the collection period did not take
316 place in the familiar surroundings but in modified metabolism cages, might have led to a
317 higher stress level that also contributed to these body mass losses. Generally, plains viscachas
318 are known to be more easily agitated than many other, smaller rodents [Weir, 1970; Kohl,
319 1980]. One possible reason for this might be body size; smaller species might more easily feel
320 protected in the shelters provided in experimental settings. In contrast, to feel protected from
321 human handlers, viscachas might have to be provided with burrows of a scale that makes
322 experimental measurements impossible.
323
324 **Adaptations to Aridity and Fossoriality**
325 Several measures in plains viscachas suggest a particular adaptation to arid environments,
326 even if the species is represented in biomes of different humidity [Jackson et al., 1996]. The
327 family Chinchillidae, to which the plains viscacha belongs together with the chinchillas
328 (*Chinchilla* spp.) and the mountain viscachas (*Lagidium* spp.), is characterized by a
329 particularly long colon [Gorgas, 1966], which indicates a high capacity for water reabsorption

330 from digesta at this site. The sizes of the digestive tract sections found in the present study
331 match those reported by Gorgas [1966]. The comparatively low water intake in the plains
332 viscachas of Exp 3 might indicate comparatively low water requirements, too, as was also
333 suggested for chinchillas [Hagen et al., 2014]. The Chinchillidae are additionally
334 characterized by the ability to produce highly concentrated urine [Weisser et al., 1970; Kohl,
335 1980].
336 In addition they have low metabolic rates [Kohl, 1980; Arends and McNab, 2001; Cortés
337 et al., 2003; Tirado et al., 2007]. At 229 $kJ/kg^{0.75}/d$, the resting metabolism of the three plains
338 viscachas of Exp 4 was below the mammalian average basal metabolic rate of 293 $kJ/kg^{0.75}/d$
339 [Kleiber, 1961], but very similar to the resting metabolic rate measured in two plains
340 viscachas by Kohl [1980] of 216 $kJ/kg^{0.75}/d$. One possible reason for a comparatively low
341 metabolism could be an adipose body condition [Earle and Smith, 1991]; given the adaptation
342 period on a roughage-only diet, the visual impression as well as palpation when transferring
343 viscachas back to their normal enclosure at the end of Exp 4, obesity appeared unlikely. A
344 generally low metabolism in fossorial mammals is usually explained as an adaptation to
345 prevent hypercapnic conditions in the burrow system [McNab, 1966; McNab, 1979].
346 Additionally, the ability to absorb a large proportion of Ca from the gut [Hagen et al., 2015]
347 and excrete Ca bound to carbonate via urine should be advantageous for fossorial animals, as
348 it allows the excretion of CO_2 without increasing the hypercapnic load of the environment
349 [Haim et al., 1985; Haim et al., 1987]. The fact that some of the excreted CO_2 was not
350 exhaled but bound in urine could partly explain the low respiration quotients measured in the
351 present study (Table 6) as the animals consumed some food in the respiration chambers
352 (which would usually lead to the expectation of a higher respiration quotient). The low
353 metabolic rate of the species is also evident in the lower estimate of DE requirements in Exp 2
354 (Fig. 7). Estimated DE requirements averaged at 445 $kJ/kg^{0.75}/d$, which is at the lower end of
355 the average range estimated for mammalian hindgut fermenters of 440-660 $kJ/kg^{0.75}/d$ [Clauss

et al., 2005]. However, these DE requirements are distinctly higher than the total metabolic rate of 298 $kJ/kg^{0.75}/d$ found in the three animals subjected to measurements in the respiration chambers (Table 6), although the two experiments were carried out at the same environmental temperatures. Whether this discrepancy is due to a particular inactivity, or a more relaxed state, in the respiration chambers, remains an open question.

Colonic Separation Mechanism and Coprophagy

As in other hystricomorph rodents, which all have a colonic furrow [Gorgas, 1966], and also in muroid rodents, there was no difference in the MRT of solute and particle markers in plains viscachas. These results corroborate that, in contrast to the colonic separation mechanism of rabbits, no fluid 'wash-back' is involved in the 'mucus trap' separation mechanisms in these groups [Hume and Sakaguchi, 1991].

The results of this experiment show that viscachas are flexible in their coprophagic behavior. To our knowledge, the flexibility of coprophagy as part of the overall digestive strategy in small herbivores is little explored so far, except for rabbits. In rabbits, it was shown that cecotroph production, or the contribution of cecotrophs to overall intake, increased with increasing dietary fiber and decreasing dietary protein concentrations [Fekete and Bokori, 1985; Carabaño et al., 1988; García et al., 1995]. Fekete and Bokori [1985] actually demonstrated that rabbits ingested a lower proportion of their cecotrophs when fed on low-fiber, high-protein diets, likely because the need to exploit microbial protein produced in the hindgut is lower. The finding that the excretion patterns of MRT markers indicated less coprophagic incidents in plains viscachas on the diets richer in protein suggests that a similar mechanism may influence the choice to practice coprophagy in other small herbivores, too.

Susceptibility to Diabetes and Diets Fed in Captivity

The observation that plains viscachas are susceptible to diabetic states when fed diets high in easily digestible carbohydrates was confirmed in the present study. Similar to free-ranging animals investigated by Wenker et al. [2007], urine tested negative for glucose on forage-only diets (Exp 2A, Exp 3A/C), but glucosuria was evident in individual animals on energy-dense diets (Exp 2B, Exp 3B). The serum glucose in all animals, and fructosamine levels in Exp 2, were within the reference range (4.7-11.2 mmol/L for glucose and 161-297 µmol/L for fructosamine) determined in free-ranging plains viscachas [Wenker et al., 2007]. In contrast, fructosamine levels in Exp 3 were above these levels, for both the forage-only and the concentrate diet, indicating that repeated measures of the same individuals may yield more important information than a comparison with reference ranges. In Exp 3B, the extremely wide range of urinary glucose as well as the high standard deviation for serum glucose and fructosamine underline a large inter-individual variety in the response to energy-dense diets. In sand rats (*Psammomys obesus*), another rodent species with a high susceptibility to diabetes and cataract formation, individual differences in susceptibility to the problem due to hereditary factors have been demonstrated [Kalman et al., 1993; Walder et al., 2000] and might also play a role in plains viscachas.

Fecal nitrogen (FN) concentrations in free-ranging viscachas ranged between 1.2 and 1.9 % of DM [Branch et al., 1994], with data from forage-only diets of Exp 2 and 3 being well within this range, the concentrate diet in Exp 3B at the upper end of it, and both the lucerne hay diet of Exp 4 and the concentrate diet in Exp 2B well above it. The FN is related to the digestibility of the diet in herbivores [Steuer et al., 2014; Gálvez-Cerón et al., 2015], as is also evident in the data of the plains viscacha of the present study. This comparison indicates that the concentrate diets used in the present study are more digestible than the diets plains viscachas probably have adapted to over evolution. The relevance of maintaining rodents susceptible to diabetic conditions on high-fiber diets without concentrates has been repeatedly recommended in order to prevent obesity and diabetes, and this not only with respect to

viscachas [Gull et al., 2009; Wenker et al., 2009] but also for degus [Edwards, 2009], tuco-tucos (*Ctenomys talarum*) [Wise et al., 1972], agoutis (*Dasyprocta* spp.) [McWilliams, 2009], and sand rats [Kalman et al., 1993].

Digestive Efficiency for Nutrients and Minerals in Comparison with other Herbivore Species

In theory, it could be expected that in animals that practice coprophagy should have particularly high apparent digestion coefficients for those nutrients that are abundant in microbes, such as protein, lipids, and phosphorus, because coprophagy serves mainly to re-ingest microbial matter otherwise lost with feces. However, a comparison of the results of the present study with literature data do not reveal any systematic differences in this respect between the horse and the coprophageous mammals. Similarly, no differences in metabolic FN losses could be demonstrated in a survey of various mammalian digestion strategies including coprophageous and non-coprophageous hindgut fermenters and ruminant and non-ruminant foregut fermenters [Schwarm et al., 2009]. The apparent digestibility of protein also did not differ noticeably between foregut-fermenting hippopotamuses and large hindgut fermenters [Schwarm et al., 2006] or between various hindgut-fermenting suids and foregut-fermenting tayassuids [Clauss et al., 2008]. Therefore, there really might be no systematic differences in the apparent digestibility of microbe-related nutrients between foregut and hindgut fermenters, or between coprophageous and non-coprophageous hindgut fermenters. This hypothesis still requires a theoretical explanation. Comparative studies using a multitude of data sources might be more suitable to detect differences in fiber digestion and intake limitation [Justice and Smith, 1992; Clauss et al., 2010a; Clauss et al., 2015]. In contrast, differences in apparent digestibility of microbe-related nutrients, i.e. in both the true digestibility and in the endogenous/metabolic fecal losses, might be too delicate to be reflected in broad comparative approaches that collate data from various sources [Hagen et

al., 2015], and would have to be investigated in carefully designed comparative feeding experiments.

Another potential assumption concerning differences between horses and the smaller herbivores relates to theories on the influence of body mass on herbivore digestive capacity [Demment and Van Soest, 1985]. An increase in dietary crude fiber content does not affect organic matter digestibility as much in horses as in rabbits or guinea pigs [Hagen et al., 2015]. This could be explained by the generally longer particle MRT in horses amounting to 23-34 h [Clauss et al., 2014] as compared to 15 h in rabbits and 18 h in guinea pigs [Franz et al., 2011a]. The MRT recorded in viscachas in the present study was, at 23-30 h (Table 3), similar to that of horses. The absence of a difference in the effect of fiber on digestive efficiency between horses and plains viscachas (Fig. 5) could thus partially be explained by the similarity of particle MRT between the two species. The combination of these long retention times and the higher degree of ingesta particle size reduction in plains viscachas as compared to horses [Fritz et al., 2009] might also explain the level of methane production in this species, which is higher than expected for the plains viscacha's body mass based on comparative data from horses, rabbits and guinea pigs [Franz et al., 2011b]. Another potential reason could lie in differences in the composition of the gut microbes. Although the plains viscacha has a higher body mass than rabbits and guinea pigs, the difference in body size to horses evidently is of a much higher magnitude, indicating that a small body size as such represents no compulsory limitation for the ability to digest fibrous diets. Actually, many small herbivores might rather have lost the ability to use such diets because of the ecological opportunity to often select higher quality diets [Clauss et al., 2013].

Conclusions

1. Plains viscachas have a lower mean resting metabolic rate than other similar sized mammals and low maintenance energy requirements, which might make the species susceptible to obesity in captivity.
2. When kept on high proportions of energy-dense feeds, plains viscachas excrete glucose in their urine, confirming the suspected link between such feeds and diabetic conditions in this species.
3. The similarity of several measures of digestive physiology in plains viscachas and domestic horses suggests that body size itself is not strictly related to digestive physiology, and that an influence of coprophagy is difficult to detect.

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Figure 1. Macroscopic anatomy of the digestive tract of plains viscacha (*Lagostomus maximus*), with photographic documentation of a complete digestive tract and the colonic furrow on the inside of the cranial part of the colon ascendens, as well as a schematic graphic representation (drawn by Jeanne Peter). Scale bars on the left indicate 10 cm.

Figure 2. Total water intake (from diet and drinking water) by plains viscachas (*Lagostomus maximus*) fed on diets with only dry components (dry forages, dry commercial feeds) (mean ±SD of the ratio of water : dry matter 1.2 ±0.3 : 1) of the present study, and literature data for rabbits (*Oryctolagus cuniculus*; 2.3 ±0.8 :1), guinea pigs (*Cavia porcellus*; 6.6 ±5.7 : 1), degus (*Octodon degus*; 2.3 ±0.5 : 1) and chinchillas (*Chinchilla laniger*; 2.0 ±0.9 : 1) [Schwabe, 1995; Wenger, 1997; Schröder, 2000; Wolf et al., 2003; Tschudin et al., 2011; Clauss et al., 2012; Hansen, 2012; Hommel, 2012; Hagen et al., 2014].

Figure 3. Postural behavior observed sporadically in plains viscachas (*Lagostomus maximus*) of the present study suggestive of coprophagy.

Figure 4. Exemplary excretion patterns for a solute (Co) and a particle (<2mm, Cr) marker in plains viscachas (*Lagostomus maximus*) in (A) Exp 2A – grass hay, (B) Exp 2B – a diet of pellets, carrots and grass hay, (C) Exp 3A – grass hay, (D) Exp 4 – lucerne hay.

Figure 5. Relationship of dietary crude fibre and the apparent digestibility (aD) of organic matter (OM) in plains viscachas (*Lagostomus maximus*) of the present study, and literature data for horses (*Equus caballus*), rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) [data collection from Hagen et al., 2015].

Figure 6. Relationship of dietary nutrient/mineral content (protein, ether extract, sodium Na, potassium K, calcium Ca and phosphorus P) and the digestible nutrient/mineral content in the experiments with plains viscachas (*Lagostomus maximus*) of the present study, and literature data for horses (*Equus caballus*), rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) for protein and ether extracts [Slade and Hintz, 1969; Sakaguchi et al., 1987; Sakaguchi and Hume, 1990; Sakaguchi et al., 1992a; Sakaguchi and Nabata, 1992; Sakaguchi et al., 1992b; Sakaguchi and Ohmura, 1992; Schwabe, 1995; Meyer et al., 1996; Wenger, 1997; Zeyner and Kienzle, 2002; Zumbrock, 2002; Clauss et al., 2012; Hommel, 2012]. Data collection for minerals from Hagen et al. [2015].

730 Table 1. Anatomical measures of the digestive tract of two male and two female adult plains viscachas
731 (*Lagostomus maximus*)

	---------- Male ----------			---------- Female ----------		
Body mass (kg)	4.5/ 4.3			2.4/4.0		
Body length (cm)	56/53			43/52		
	Length (cm)	Empty mass (g)	Wet mass content (g)	Length (cm)	Empty mass (g)	Wet mass content (g)
Stomach	8/11	nd/23	nd/58	12/10	8/21	44/120
Small intestine	292/381	nd/44	nd/85	280/289	16/ 44	25/ 62
Caecum	15/15	nd/30	nd/217	16/10	13/21	212/75
Colon ascendens	28/49	nd/14	nd/43	29/27	8/19	39/38
Remainder of colon and rectum	216/213	nd/94	nd/32	217/130	15/13	36/24

732 nd, not determined
733

Table 2. Nutrient composition (g/kg dry matter [DM]) and gross energy (MJ/kg DM) content of feeds and leftovers from three feeding experiments with plains viscachas (*Lagostomus maximus*)

	Exp 2			Exp 3			Exp 4		
	Grass hay	Pellets[1]	Carrots	Grass hay	Hay leftovers	Pellets[2]	Lucerne hay	Hay leftovers	Pellets[3]
Total ash	43	84	77	48 ±6	53 ±9	104	73 ±10	100 ±19	121
Crude protein	47	255	55	73 ±5	75 ±8	147	120 ±19	149 ±13	163
Ether extract	10	48	23	14 ±1	14 ±3	35	7 ±0	8 ±1	16
Crude fiber	449	132	92	392 ±22	397 ±27	17	469 ±35	418 ±62	298
NDF	742	223	118	653 ±22	657 ±19	323	642 ±40	568 ±45	455
ADF	438	126	83	352 ±20	347±29	180	515 ±29	466 ±55	354
ADL	42	17	0	27 ±7	26 ±7	38	122 ±9	106 ±11	97
Gross energy	18.7	19.2	17.8	18.6 ±0.2	18.5±0.2	17.9	18.0 ±0.2	17.6 ±0.5	17.8

[1]Commercial guinea pig diet containing grains, soybean meal, molasses, grass meal, mineral premix (Meerschweinchen Zucht 3500 Nafag 9211, Provimi Kliba SA, Kaiseraugst, Switzerland).

[2]Commercial guinea pig diet containing grains, soybean meal, molasses, grass meal, mineral premix (Ergänzungsfutter für Meerschweinchen Melior 4653, Meliofeed AG, Herzogenbuchsee, Switzerland).

[3]Pelleted lucerne (No. 2805, Provimi Kliba SA, Kaiseraugst, Switzerland)

NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin

Table 3. Mean (±standard deviation) body mass (BM), food dry matter (DM), digestible energy (DE) and water intake, mean retention times of a particle (MRT Cr) and a solute (MRT Co) marker, and nutrient composition of the ingested diet in the different treatments of this study

	----- Exp 2 (n=7) -----		---------- Exp 3 (n=6) ----------			Exp 4 (n=3)
	A	B	A	B	C	
BM (kg)	3.53 ±1.11	3.50 ±0.96	3.16 ±0.81	3.72 ±1.00	3.27 ±0.79	4.47 ±1.77
BM change (g/d)	-8.7 ±9.3	16.3 ±9.8	-12.7 ±5.7	-22.1 ±7.7	-13.2 ±7.5	nd
DM intake ($g/kg^{0.75}/d$)	47 ±8	50 ±6	51 ±9	38 ±11	43 ±8	45 ±11
DE intake ($kJ/kg^{0.75}/d$)	307 ±152	629 ±83	496 ±84	446 ±131	355 ±69	441 ±135
Total water intake ($g/kg^{0.75}/d$)	nd	nd	62 ±20	39 ±16	58 ±18	nd
MRT Cr (h)	26 ±6	30 ±10	28 ±5	nd	nd	24 ±2
MRT Co (h)	26 ±6	31 ±8	28 ±3	nd	nd	23 ±3
Hay (% of total DM intake)	100	23 ±6	100	29 ±12	100	73 ±2
Diet composition (g per kg DM)						
Total ash	43	74 ±2	46 ±4	85 ±10	44 ±3	53 ±10
Crude protein	47	192±12	66 ±6	126 ±10	72 ±7	100 ±21
Ether extract	10	38 ±2	15 ±4	29 ±3	15 ±2	9 ±3
Crude fiber	449	202 ±21	351 ±27	246 ±40	392 ±26	485 ±58
NDF	742	334 ±34	604 ±16	433 ±35	666 ±15	676 ±18
ADF	438	194 ±21	320 ±14	244 ±22	364 ±22	532 ±48
ADL	42	22 ±2	18 ±0	38 ±0	30 ±0	135 ±16
Gross energy (MJ per kg DM)	18.7	18.9 ±0	18.5 ±0.2	18.3 ±0.2	18.9 ±0.1	18.4 ±0.9
Na	1.4	3.9 ±0.2	0.3 ±0	6.4 ±1.0	0.5 ±0.1	nd
K	13.8	20.5 ±0.6	14.8 ±2.4	11.3 ±0.3	15.2 ±4.0	nd
Ca	4.7	10.1 ±0.5	4.7 ±0.7	15.8 ±1.8	3.7 ±0.9	nd
P	2.0	5.4 ±0.3	2.8 ±0.3	5.7 ±0.6	2.4 ±0.4	nd
Mg	1.5	2.9 ±0.1	1.9 ±0.3	1.8 ±0.2	1.5 ±0.2	nd
Cu (mg per kg DM)	3.8	14.3 ±0.9	3.2 ±1.6	29.4 ±4.1	5.7 ±0.5	nd
Zn (mg per kg DM)	21.4	58.5 ±3.2	21.9 ±6.4	116.7 ±16.6	19.6 ±7.8	nd

nd, not determined; NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin

for Exp 2, no standard deviation for hay composition is given because leftovers were not analysed

in Exp2 and Exp3, treatments (A, B, C) represent differences in the proportions of hay and concentrates

749 Table 4. Fecal dry matter (DM) excretion, fecal nitrogen, urine output and apparent digestibilities, in the different treatments of
750 this study

	----- Exp 2 (n=7) -----		---------- Exp 3 (n=6) ----------			Exp 4 (n=3)
	A	B	A	B	C	
Dry matter defecation ($g/kg^{0.75}/d$)	28 ±9	17 ±4	23 ±5	13 ±4	24 ±5	20 ±2
Fecal nitrogen (%DM)	1.53 ±0.14	2.76 ±0.36	1.43 ±0.09	1.93 ±0.43	1.35 ±0.08	2.28 ±0.15
Metabolic fecal nitrogen (%DM)	0.87 ±0.14	1.99 ±0.39	nd	nd	nd	nd
Urine excretion ($g/kg^{0.75}/d$)	nd	nd	8.5 ±3.5	7.2 ±5.9	6.2 ±1.7	nd
Apparent digestibility (%)						
DM	45 ±4	66 ±7	54 ±4	65 ±5	45 ±4	55 ±6
Organic matter	46 ±4	68 ±7	55 ±4	66 ±5	46 ±4	57 ±5
Crude protein	-14 ±14	70 ±4	38 ±6	66 ±9	34 ±9	26 ±16
Ether extract	-30 ±16	75 ±6	34 ±13	72 ±6	24 ±15	-23 ±104
Crude fiber	45 ±7	40 ±14	41 ±7	47 ±11	39 ±5	56 ±4
NDF	44 ±5	40 ±14	45 ±5	50 ±7	39 ±4	55 ±5
ADF	47 ±5	39 ±13	42 ±7	50 ±8	36 ±7	56 ±2
Gross energy	42 ±4	66 ±7	53 ±4	65 ±5	44 ±4	53 ±5
Na	59 ±4	81 ±5	4 ±25	93 ±1	55 ±8	nd
K	64 ±11	88 ±3	85 ±5	91 ±3	76 ±7	nd
Ca	-12 ±16	2 ±14	6 ±11	35 ±10	-76 ±55	nd
P	-7 ±12	1 ±15	40 ±12	19 ±14	0 ±23	nd
Mg	35 ±6	45 ±7	52 ±6	51 ±5	50 ±16	nd
Cu	-23 ±12	3 ±13	-99 ±141	55 ±6	49 ±17	nd
Zn	-12 ±10	4 ±14	-33 ±44	8 ±18	-146 ±174	nd

751 nd, not determined; NDF, neutral detergent fiber; ADF, acid detergent fiber
752 in Exp2 and Exp3, treatments (A, B, C) represent differences in the proportions of hay and concentrates (cf. Table 3)

Table 5. Parameter estimates (with 95% confidence intervals) for regression equations according to y = a + bx (indicated as y-x) in various herbivore species from the present study and the literature [data collection from Hagen et al., 2015]

		aDOM-CF	dCP-CP	dEE-EE	dNa-Na	dK-K	dCa-Ca	dP-P	dMg-Mg	dCu-Cu	dZn-Zn
Viscacha	a	82.1 [74.2;89.9]	-43.7 [-53.7;-33.7]	-12.3 [-1.4;-1.1]	-0.035 [-0.045;-0.025]	-0.222 [-0.466;0.022]	-0.418 [-0.584;-0.252]	-0.002 [-0.072;0.068]	0.002 [-0.022;0.025]	-0.374 [-0.550;-0.197]	-1.171 [-1.883;-0.459]
	b	-0.75 [-0.97;-0.53]	0.93 [0.84;1.01]	1.09 [1.02;1.16]	0.95 [0.92;0.98]	0.96 [0.80;1.11]	0.54 [0.36;0.72]	0.12 [-0.06;0.29]	0.46 [0.34;0.57]	0.61 [0.49;0.72]	0.18 [0.06;0.30]
Rabbit	a	91.4 [87.2; 95.5]	-25.4 [-43.7;-7.2]	-6.8 [-12.2;-1.4]	-0.017 [-0.025;-0.010]	0.029 [-0.042; 0.099]	-0.147 [-0.201;-0.092]	-0.146 [-0.246;-0.047]	-0.079 [-0.109;-0.048]	nd	nd
	b	-1.70 [-1.91; -1.49]	0.86 [0.75;0.97]	0.86 [0.71;1.02]	0.98 [0.96;1.00]	0.88 [0.84;0.92]	0.76 [0.73;0.79]	0.58 [0.35;0.81]	0.84 [0.72;0.95]	nd	nd
Guinea pig	a	99.7 [88.3; 111.0]	-37.9 [-58.2;-17.8]	-7.0 [-10.0;-3.9]	0.023 [-0.032; 0.078]	0.338 [0.056; 0.619]	-0.032 [-0.106; 0.043]	-0.117 [-0.157; -0.078]	0.013 [-0.017; 0.043]	nd	nd
	b	-1.84 [-2.37; -1.30]	0.89 [0.76;1.02]	0.88 [0.80;0.97]	0.42 [0.10; 0.75]	0.46 [0.31; 0.62]	0.87 [0.74; 1.00]	0.85 [0.75; 0.94]	0.63 [0.40; 0.86]	nd	nd
Degu	a	90.0 [82.0; 97.9]	-43.7 [-53.7;-33.7]	-7.7 [-13.1;-2.3]	0.002 [-0.015; 0.019]	-0.167 [-0.199; -0.135]	-0.428 [-0.649; -0.207]	-0.176 [-0.501; 0.149]	0.085 [-0.148; 0.318]	nd	nd
	b	-1.48 [-1.96; -1.00]	0.93 [0.84;1.01]	0.99 [0.86;1.11]	0.89 [0.80; 0.98]	1.01 [0.99; 1.02]	0.76 [0.60; 0.91]	0.53 [-0.04; 1.09]	0.16 [-0.71; 1.04]	nd	nd
Chinchilla	a	83.4 [74.9; 92.0]	-60.9 [-90.5;-31.4]	-5.2 [-18.9;8.5]	nd	nd	-0.027 [-0.048; 0.102]	-0.314 [-0.450; -0.177]	nd	nd	nd
	b	-1.31 [-1.75; -0.87]	1.02 [0.84;1.19]	0.86 [0.30;1.42]	nd	nd	-0.01 [-0.07; 0.06]	0.83 [0.49; 1.18]	nd	nd	nd
Horse	a	88.6 [85.4; 91.8]	-21.7 [-30.2;-13.1]	-1.5 [-4.9;1.9]	-0.052 [-0.068; -0.036]	-0.118 [-0.153; -0.083]	-0.020 [-0.088; 0.048]	-0.121 [-0.153; -0.088]	0.039 [0.030; 0.049]	-0.033 [-0.368;0.302]	-0.735 [-3.475;2.005]
	b	-1.06 [-1.18; -0.95]	0.85 [0.78;0.93]	0.46 [0.36;0.55]	0.84 [0.78; 0.89]	0.88 [0.86;0.90]	0.40 [0.34; 0.46]	0.44 [0.37; 0.51]	0.12 [0.07; 0.16]	0.33 [0.18;0.48]	0.00 [-0.38;0.38]

aDOM, apparent digestibility of organic matter (%); CF, crude fiber (in % of DM); CP, crude protein, EE, ether extract (in g kg DM^{-1}); Na, sodium; K, potassium; Ca, calcium; P, phosphorus; Mg, magensium (in % of DM); Cu, copper; Zn, zinc (in mg g DM^{-1}); d indicates 'apparently digestible' mineral; nd, not determined.

Table 6. Gaseous exchange, metabolic rate and respiratory quotient in individual plains viscachas (*Lagostomus maximus*)

Individual		1	2	3
O_2 consumption	L/d	33.9	50.5	47.4
Metabolic rate	kJ/kg$^{0.75}$/d	313	342	238
Resting metabolic rate	kJ/kg$^{0.75}$/d	244	250	194
CO_2 excretion	L/d	27.8	39.1	36.1
Respiratory quotient*		0.82	0.77	0.76
CH_4 excretion	L/d	1.61	2.74	1.67
	L/kg BM/d	0.57	0.64	0.26
	L/kg DMI/d	13.0	21.9	11.7
	% GE intake	2.89	4.90	2.40
	% DE intake	4.95	9.74	4.75
	L/kg dNDF intake/d	31.7	57.1	36.2

*Calculated as CO_2/O_2.

BM, body mass; DMI, dry matter intake; GE, gross energy; DE digestible energy; dNDF, digestible neutral detergent fiber

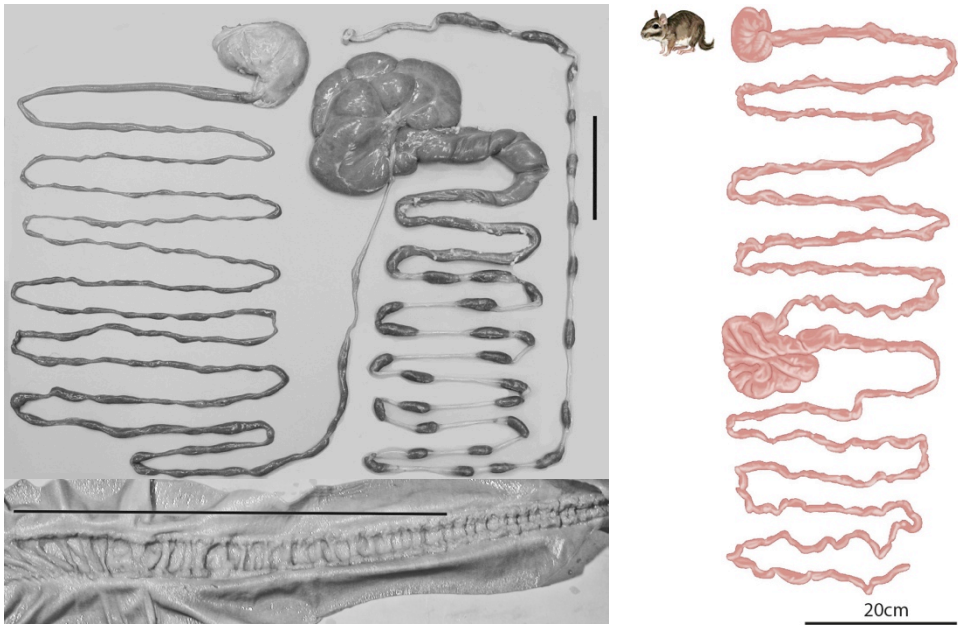

Figure 1. Macroscopic anatomy of the digestive tract of plains viscacha (*Lagostomus maximus*), with photographic documentation of a complete digestive tract and the colonic furrow on the inside of the cranial part of the colon ascendens, as well as a schematic graphic representation (drawn by Jeanne Peter). Scale bars on the left indicate 10 cm.

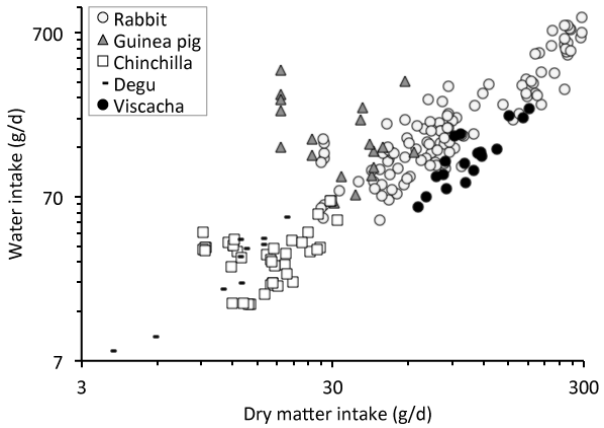

Figure 2. Total water intake (from diet and drinking water) by plains viscachas (*Lagostomus maximus*) fed on diets with only dry components (dry forages, dry commercial feeds) (mean ±SD of the ratio of water : dry matter 1.2 ±0.3 : 1) of the present study, and literature data for rabbits (*Oryctolagus cuniculus*; 2.3 ±0.8 :1), guinea pigs (*Cavia porcellus*; 6.6 ±5.7 : 1), degus (*Octodon degus*; 2.3 ±0.5 : 1) and chinchillas (*Chinchilla laniger*; 2.0 ±0.9 : 1) [Schwabe, 1995; Wenger, 1997; Schröder, 2000; Wolf et al., 2003; Tschudin et al., 2011; Clauss et al., 2012; Hansen, 2012; Hommel, 2012; Hagen et al., 2014].

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780 Figure 3. Postural behavior observed sporadically in plains viscachas (*Lagostomus maximus*)
781 of the present study suggestive of coprophagy.
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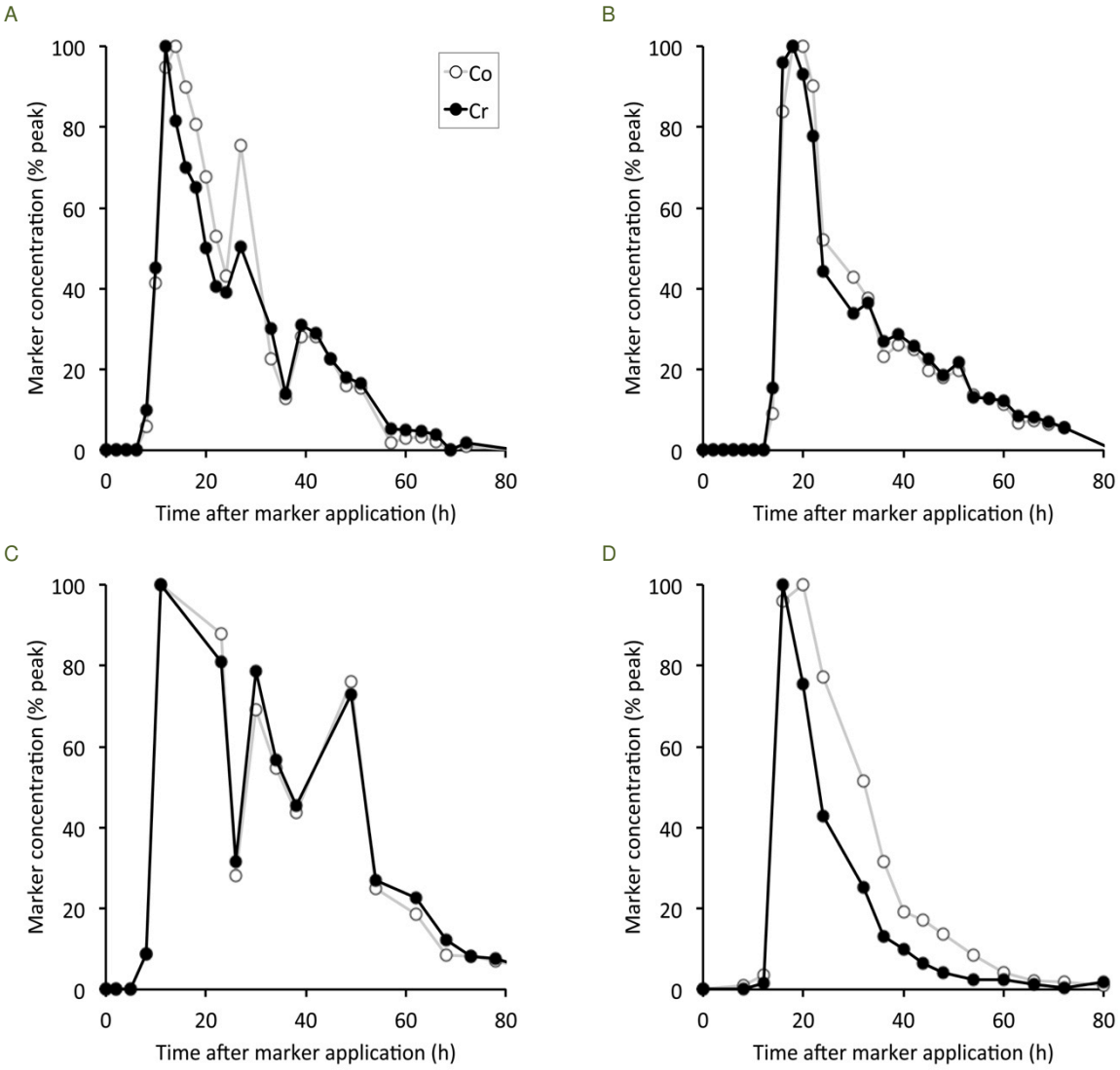

784 Figure 4. Exemplary excretion patterns for a solute (Co) and a particle (<2mm, Cr) marker in
785 plains viscachas (*Lagostomus maximus*) in (A) Exp 2A – grass hay, (B) Exp 2B – a diet of
786 pellets, carrots and grass hay, (C) Exp 3A – grass hay, (D) Exp 4 – lucerne hay.
787

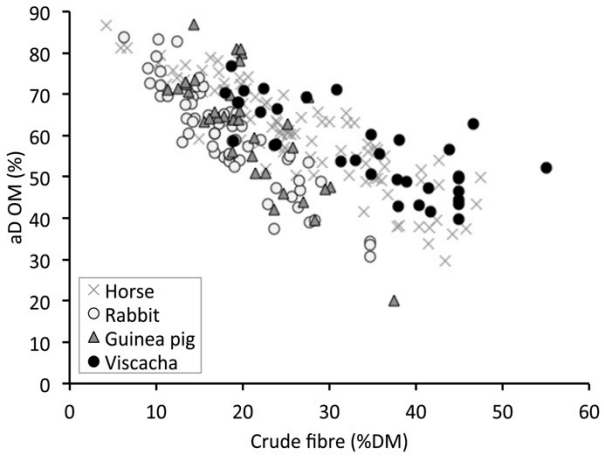

Figure 5. Relationship of dietary crude fibre and the apparent digestibility (aD) of organic matter (OM) in plains viscachas (*Lagostomus maximus*) of the present study, and literature data for horses (*Equus caballus*), rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) [data collection from Hagen et al., 2015].

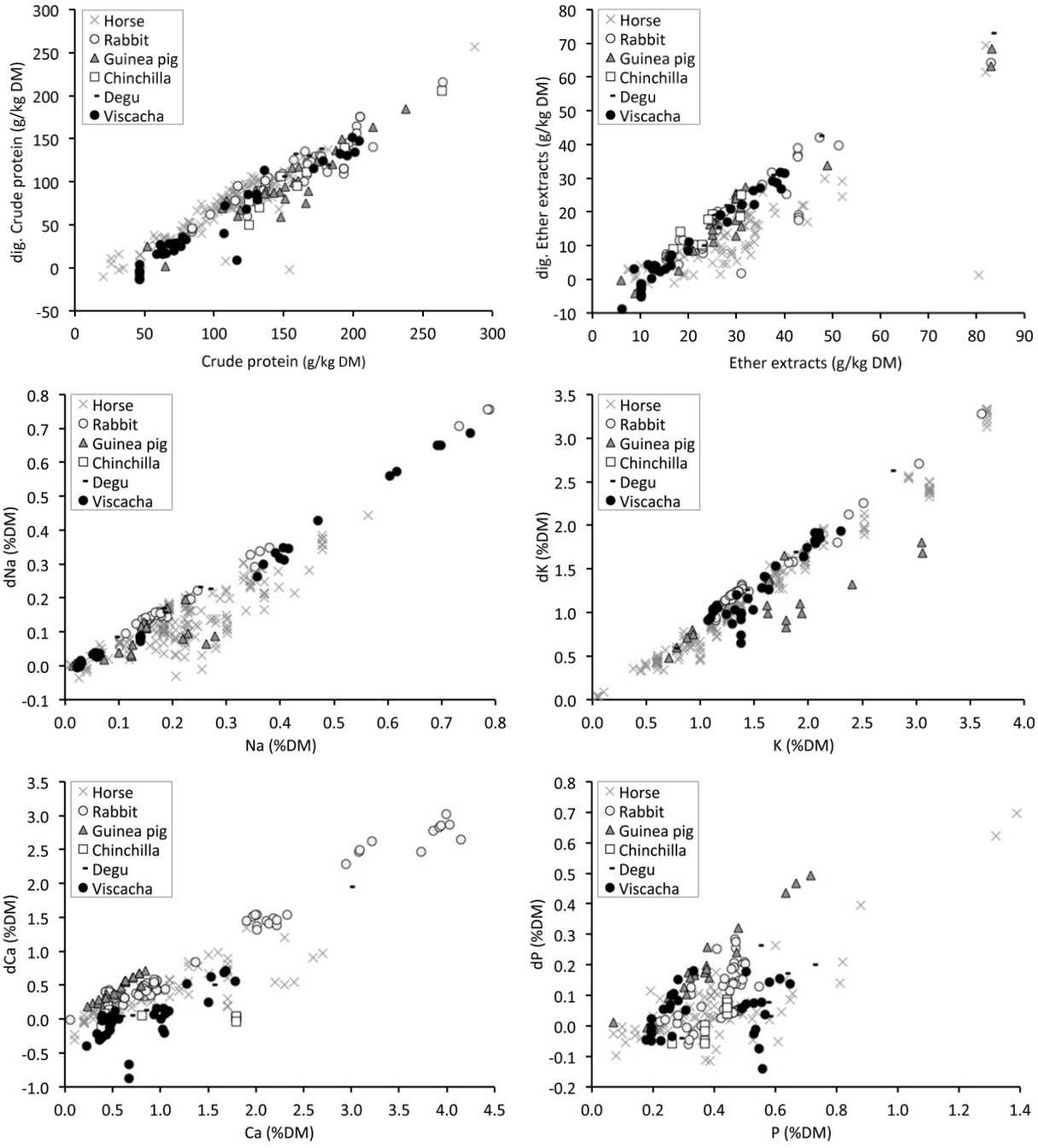

Figure 6. Relationship of dietary nutrient/mineral content (protein, ether extract, sodium Na, potassium K, calcium Ca and phosphorus P) and the digestible nutrient/mineral content in the experiments with plains viscachas (*Lagostomus maximus*) of the present study, and literature data for horses (*Equus caballus*), rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) for protein and ether extracts [Slade and Hintz, 1969; Sakaguchi et al., 1987; Sakaguchi and Hume, 1990; Sakaguchi et al., 1992a; Sakaguchi and Nabata, 1992; Sakaguchi et al., 1992b; Sakaguchi and Ohmura, 1992; Schwabe, 1995; Meyer et al., 1996; Wenger, 1997; Zeyner and Kienzle, 2002; Zumbrock, 2002; Clauss et al., 2012; Hommel, 2012]. Data collection for minerals from Hagen et al. [2015].

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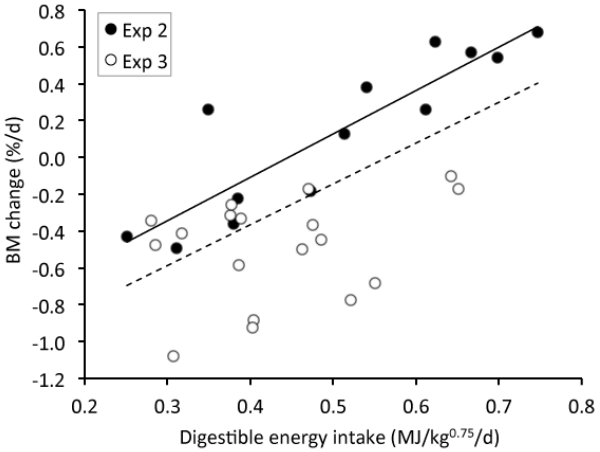

808 Figure 7. Relationship between the daily intake of digestible energy and body mass changes
809 as the basis for the estimation of maintenance energy requirements in plains viscachas
810 (*Lagostomus maximus*) from two of the experiments carried out in the present study where
811 animals were kept at different ambient temperatures (Exp 2: 20-22°C; Exp 3: 5-10°C).
812 Straight line – regression for Exp 2; interrupted line – regression for both experiments
813 combined.